

Trapping of *Rhizophora mangle* Propagules by Coexisting Early Successional Species

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Abstract Distributions of mangroves in coastal wetlands are influenced by abiotic conditions and the net effect of biotic interactions, including competition, facilitation, and consumer pressure. In coastal wetlands, early successional shrubs, herbs, and grasses may facilitate recruitment of mangroves through multiple mechanisms, including amelioration of environmental conditions, propagule trapping, and structural support. In Mosquito Lagoon, FL, we observed an aggregated distribution of *Rhizophora mangle* propagules along vegetated shorelines with *Batis maritima* and *Sarcocornia perennis* and hypothesized that this distribution was a result of propagule trapping by the vegetation. We designed a field experiment to evaluate retention of *R. mangle* propagules on vegetated and unvegetated shorelines in Mosquito Lagoon. Significant differences were found in the retention time of mangrove propagules at each shoreline type, with vegetated shorelines retaining propagules significantly longer than unvegetated shorelines. Results from this study help to define facilitative mechanisms which may be important in successional processes of coastal wetlands and have direct restoration applications. Successful recovery of mangroves at restoration sites may be facilitated by establishment of *B. maritima* and *S. perennis*, when natural propagule sources are available, or through planting mangrove seedlings into existing stands of these halophytes when restoration areas are propagule-limited.

Keywords *Batis maritima* · Facilitation · Mangrove restoration · Nurse plants · *Sarcocornia perennis*

Introduction

Mangrove distributions in tropical and subtropical coastal wetlands are influenced by tolerances to abiotic conditions and direct and indirect effects of community interactions, including competition, facilitation, and consumer pressure (Odum and McIvor 1990; McKee 1995; Duke et al. 1998; Lacerda et al. 2001; Alongi 2009). In subtropical coastal wetlands, halophytic shrubs, grasses, and herbs can be found growing with mangroves, but the role of positive community interactions on growth, recruitment, and distribution of many mangrove species is still largely unknown (Stevens et al. 2006). Positive interactions potentially have an important role in natural regeneration, and understanding the biotic processes affecting mangrove species is critical for future conservation, restoration, and management of mangrove ecosystems worldwide (Milbrandt and Tinsley 2006; Stevens et al. 2006; Moreno-Mateos et al. 2012; Peterson and Bell 2012).

An estimated 35 % of global mangrove area was lost between 1980 and 2000 (Giri et al. 2011), threatening survival of associated organisms and decreasing crucial ecosystem services (Alongi 2009). In response to loss of mangrove habitat, restoration has increased in recent decades; however, mangrove ecosystems are often slow to recover and may require decades before structure and ecosystem function are similar to reference conditions (McKee and Faulkner 2000; Lewis 2005; Moreno-Mateos et al. 2012). One type of facilitation with important applications to ecosystem restoration involves the initial colonization of plant species, which then act as “nurse plants” for other establishing species (Niering et al. 1963; Lewis 1982, 2005; Padilla and Pugnaire 2006; Lopez et al. 2007; Brooker et al. 2008). The nurse syndrome is a type of facilitation where the seedlings are the beneficiaries of adult plants, the nurse plants, and this type of interaction can be common in early successional communities, creating an aggregated distribution of seedlings associated with the

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nurse plant (Brooker 2006; Lopez et al. 2007). Nurse plants can help secondary species overcome recruitment limitation and increase success of establishment (Young et al. 2005). Incorporating facilitation into restoration plans is becoming more common in terrestrial ecosystem restoration (Padilla and Pugnaire 2006; Halpern et al. 2007), and inclusion of positive interactions, like nurse effects, can lead to more ecologically based restoration methods (Padilla and Pugnaire 2006; Brooker et al. 2008). Restoration applications with nurse plants have been beneficial in terrestrial reforestation programs, such as degraded Mediterranean systems (Maestre et al. 2001; Castro et al. 2004; Gomez-Aparicio et al. 2004); however, inclusion of facilitative interactions has been less common in restoration of aquatic systems (Halpern et al. 2007). Identifying co-occurring plant and mangrove interactions and understanding the mechanisms driving these interactions are needed for inclusion in mangrove restoration and management plans.

In coastal wetlands, early successional plants may facilitate recruitment of mangroves through multiple mechanisms, including amelioration of environmental conditions, propagule trapping, and structural support. Milbrandt and Tinsley (2006) found that *Batis maritima* significantly increased survival of *Avicennia germinans* seedlings and attributed this positive effect on mangrove survival to greater surface elevation caused by the dense root system of *B. maritima*. McKee et al. (2007) reported positive effects of *Sesuvium portulacastrum* and *Distichlis spicata* on *Rhizophora mangle* in Belize. Both of these species increased establishment of *R. mangle* by propagule trapping, reduction of soil temperature, and improved soil aeration, but only *D. spicata* provided structural support by promoting establishment of propagules in the vertical position (McKee et al. 2007). Mangrove propagules disperse by hydrochory (water dispersal), and stranding and retention in suitable habitat are critical steps for successful establishment after dispersal (Rabinowitz 1978), which can be facilitated through trapping by emergent vegetation in riparian and estuarine habitats (Stevens et al. 2006; McKee et al. 2007; Nilsson et al. 2010; Peterson and Bell 2012). Stevens et al. (2006) found that high numbers of propagules dropped by mature mangroves (primarily *A. germinans*) were trapped within 5–15 m of parent trees by vegetation in a subtropical wetland in Florida. The salt marsh grass species *Spartina alterniflora* facilitated propagule retention in Florida wetlands and was particularly beneficial in areas where high wave energy was problematic for mangrove recruitment (Lewis 1982, 2005). Peterson and Bell (2012) found that retention of *A. germinans* propagules in vegetated patches varied with the species of plant present in the patch, with *Sporobolus virginicus* retaining significantly more propagules compared to *B. maritima* and *S. portulacastrum* in a mangrove-upland ecotone. These results suggest that location and species-specific characteristics of both the nurse plants and mangrove

species can lead to variation in the importance of different mechanisms and the outcome of interactions.

Our study tests the propagule trapping hypothesis with *R. mangle* propagules at a coastal wetland in early stages of recovery following hydrological restoration of mosquito impoundments in Mosquito Lagoon, Florida. *R. mangle* propagules are large (>30 cm) and retain buoyancy for up to 1 year (Rabinowitz 1978; Tomlinson 1994); thus, propagule trapping by shoreline vegetation may be important for retaining stranded propagules until initiation of root production, particularly during periods of prolonged flooding. During post-restoration monitoring conducted by authors at this restored mosquito impoundment, we observed higher numbers of *R. mangle* propagules in vegetated patches with initial plant colonizers compared to unvegetated shorelines. The most common shoreline vegetation containing stranded *R. mangle* propagules was a mix of two herbaceous halophytes *B. maritima* and *Sarcocornia perennis*. These commonly co-occurring species are found in coastal wetlands throughout Florida and the Caribbean (Rey 1994; Schmalzer 1995; McKee 1995; Lacerda et al. 2001; Lewis 2005; Rey et al. 2012). Both species are perennial, low-growing (height <1 m), succulent plants that create thick mats of vegetation (Tiner 1993; Taylor 1998) and were commonly the initial plant colonizers at sites monitored within 1 month of restoration in Mosquito Lagoon. Here, we present results from a field experiment to evaluate the retention of *R. mangle* propagules on vegetated and unvegetated shorelines. We hypothesized that mangrove propagules would be retained significantly longer on vegetated shorelines compared to unvegetated shorelines. Identifying biotic interactions between mangroves and associated flora has direct applications to mangrove restoration as well as increasing our understanding of the role of community interactions in structuring ecosystems.

Methods

Study Site

This study was located in Mosquito Lagoon, in Canaveral National Seashore, FL (28° 53' 05.81" N, 80° 49' 44.85" W; Fig. 1). Mosquito Lagoon is the northernmost portion of the Indian River Lagoon, a 250-km estuary located on the east coast of Florida that spans the temperate-subtropical climate boundary. Currents in Mosquito Lagoon are primarily wind-driven, and north and northwestern winds are common during fall and winter months. Water levels in Mosquito Lagoon are microtidal and change seasonally, with high water season occurring in fall and winter (Schmalzer 1995) and coinciding with dispersal time of *R. mangle* propagules. During the high water season, coastal wetlands can be flooded continuously during both high and low tides. In the 1960s, coastal wetlands

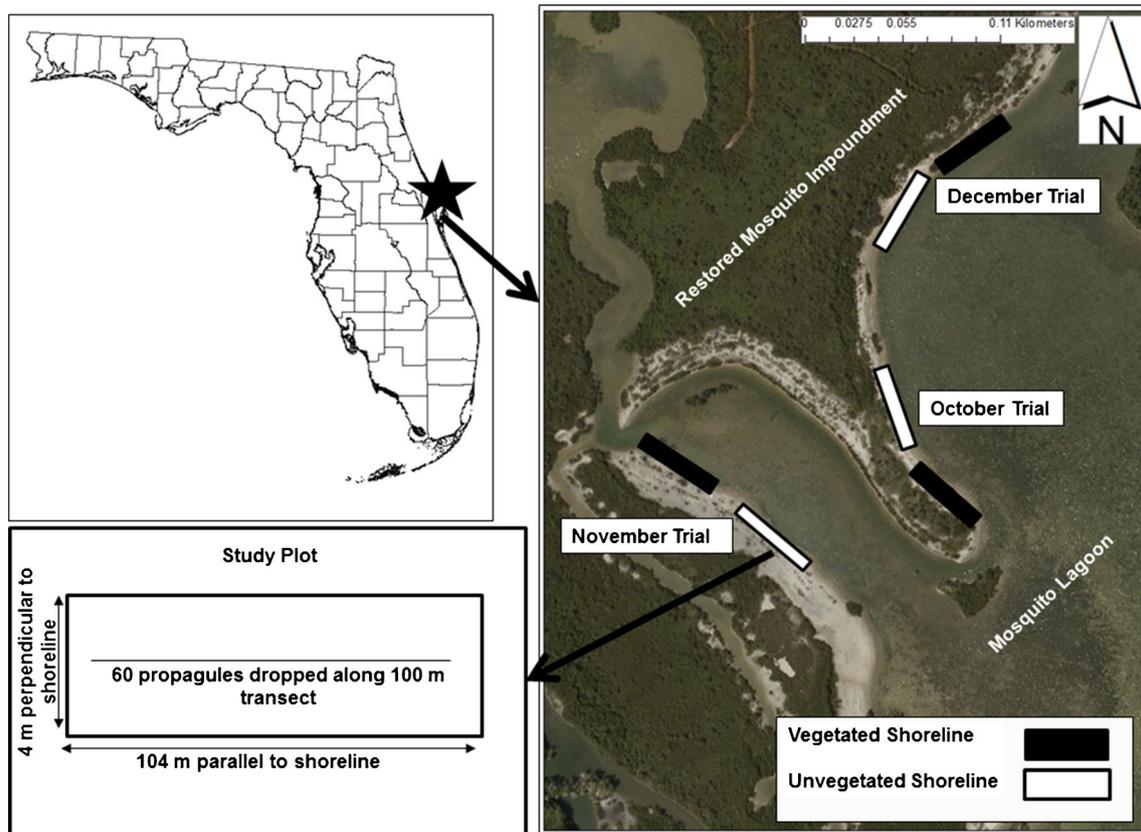


Fig. 1 Study location was a restored mosquito impoundment in Mosquito Lagoon, on the central east coast of Florida. Three pairs of study plots were established prior to the start of experiment and randomly assigned to trial start dates (October, November, December). Each study plot (vegetated, unvegetated) was 104 m in length parallel to shoreline and 4 m in

length perpendicular to shoreline. Florida map: Florida County Boundaries—Florida Statewide July 2011 layer downloaded from <http://www.fgdl.org/metadataexplorer/explorer.jsp>. Aerial photography was provided by St. Johns River Water Management District

in Mosquito Lagoon were impounded for mosquito management (Schmalzer 1995; Brockmeyer et al. 1997; Rey et al. 2012). Hydrological restoration began in the 1990s to mechanically level dikes to wetland elevations, followed by natural regeneration of native plant communities (Brockmeyer et al. 1997; Rey et al. 2012). The impoundment where this study was conducted was restored in 2003 (R. Brockmeyer, pers. comm.) and was part of a biodiversity monitoring program documenting recovery of native flora and fauna following hydrological restoration. At the time of this study, the impoundment was 7 years post-restoration and supported a patchy distribution of marsh vegetation, which provided researchers with both vegetated and unvegetated patches on shorelines in a similar geographic location (Fig. 1).

Experimental Methods

Three trials were conducted and began on the following dates: 11 October 2010 (trial 1), 1 November 2010 (trial 2), and 3 December 2010 (trial 3). The first trial was initiated after the start of seasonal high water and during annual natural *R. mangle* dispersal. Subsequent trials were spaced out to

evaluate the effects of propagule trapping over the high water season. Each trial ran for 16 weeks. Due to overlap in timing of trials to cover the time of *R. mangle* seed dispersal, different shoreline locations along the restored impoundment were used for each trial; thus, the reader is cautioned that the interpretation of the trial date variable is confounded. Locations for each trial were determined during biodiversity monitoring in summer 2010 prior to the start of the first trial and randomly assigned to one of the three trial dates. All locations were low-energy shorelines, away from major boating channels, and contained both vegetated and unvegetated areas with a minimum size of 150 m in length parallel to shoreline and 4 m in width for each shoreline type. Post-restoration monitoring included elevation measurements along a perpendicular transect using a laser level and stadia rod. Relative change in elevation from the lowest observed water level to 5 m landward was measured in 0.5-m intervals along four randomly located transects within all study plots. We initially measured seven different locations and selected three locations with similar elevations to control for the effect of elevation on the retention of propagules. All shorelines used in this study had a mean relative elevation between 12.0 and 12.5 cm (± 0.5 m

NAVD88; Table 1) that gradually sloped landward, increasing by approximately 2 % from the lowest observed water level to 4 m landward. The number of days each site was completely flooded during each trial was estimated using relative elevation measurements of restored mosquito impoundment shorelines, field observations of water depth, and minimum tide predictions from nearest the nearest tide buoy (Ponce Inlet, <http://tidesandcurrents.noaa.gov>; Fig. 2).

Rhizophora mangle propagules were collected from shorelines (post-dispersal) in non-impounded coastal wetlands in Mosquito Lagoon 24 h before the start of each trial. Propagules were examined after collection, and only those without roots or damage to the hypocotyl were used for this experiment. Propagules were randomly assigned to one of two treatments and painted with different colors (Krylon Interior-Exterior paint): pink (vegetated) and yellow (unvegetated). Prior testing showed that spray paint did not decrease survival of propagules (100 % of painted and unpainted propagules ($n=15$) produced the first set of leaves). The length of propagules was measured prior to painting.

The following methods were repeated at each vegetated and unvegetated shoreline for all trials (Fig. 1). Study plots with and without vegetation (104 m parallel to shoreline \times 4 m perpendicular to shoreline) were established at each location (Fig. 1). A linear transect was run parallel to the shoreline in the center of each study plot (Fig. 1), and 60 propagules were dropped at randomly generated locations along the transect (difference in elevations where each propagule was dropped ranged from 0 to 3 cm in all study plots). Propagules were dropped in a horizontal position at the water's surface (October and November trials) or 5 cm above the substrate when sites were dry (December trial). At each location, a propagule was dropped, and water depth was measured with a meter stick. Vegetated study plots contained a mix of *B. maritima* and *S. perennis*, and the percent cover of each species was measured using the point-intercept method in 0.25-m² quadrats (10 points per quadrat) centered on each propagule dropped along transects. After 2 days, a visual search in 2-

m-wide belt transects on the seaward and landward sides of each initial transect identified locations of retained painted propagules within the 104 m \times 4 m study plot (Fig. 1). Each *R. mangle* propagule was marked individually with a survey flag (0.9 m in height with 12.7 cm \times 12.7 cm orange flag) and ID number. During each monitoring visit, propagules were recorded as retained if present within a 0.25-m² quadrat placed on the substrate with the ID flag in the center of the quadrat. Propagule condition (viable or brown/shriveled, consumer damage), propagule orientation (horizontal or vertical), and water depth in each quadrat were also recorded. Initial setup and all post-deployment monitoring were conducted during low tide. Monitoring occurred every 2 days post-deployment for the first week and then weekly for a total of 16 weeks.

Statistical Analysis

The “survreg” function for survival analysis was used to compare the effects of two factors, shoreline type (vegetated, unvegetated) and trial start date (October, November, December), on the retention time of *R. mangle* propagules (R 2.14.1, R Development Core Team 2005; Crawley 2007). The final status was defined as either retained or lost, and data was fitted using a Weibull distribution. Simplified models were compared using the ANOVA function to detect significant changes in deviance when terms were removed. For the minimal adequate model, a likelihood-ratio test was used to identify the significant effect of factors, using the log-likelihood values given by the “survreg” function. References for contrasts were the vegetated shoreline treatment and December trial because they varied from the first two trials in initial water depth and number of days flooded (see Results below). One-way ANOVA was used to compare percent cover of *B. maritima* and *S. perennis* at the initial vegetated quadrats along each transect ($n=60$ per trial) for the three trial dates (R 2.14.1, R Development Core Team 2005; Crawley 2007). For all statistical analyses, minimum p value for evaluating significance was 0.05.

Table 1 Means (\pm SE) for initial propagule length (cm), elevation of study plots (cm), water depth at start of trial (cm), and the estimated number of days sites were submerged at both high and low tides for each trial date and shoreline treatment

Trial start date	Mangrove dispersal season	Shoreline type	Mean length of propagules (cm \pm SE)	Mean relative change in elevation (cm \pm SE)	Mean water depth at start of trial (cm \pm SE)	Time sites submerged for full tide cycle (days)
11 October 2010	Early dispersal season	Vegetated	30.5 \pm 0.2	12.3 \pm 2.1	4.7 \pm 0.2	33
		Unvegetated	30.7 \pm 0.3	12.5 \pm 2.2	5.9 \pm 0.3	33
1 November 2010	Mid-dispersal season	Vegetated	30.7 \pm 0.3	12.0 \pm 2.1	4.8 \pm 0.3	20
		Unvegetated	31.3 \pm 0.3	12.1 \pm 1.8	5.2 \pm 0.3	20
3 December 2010	Late dispersal season	Vegetated	31.3 \pm 0.4	12.3 \pm 1.2	0.0 \pm 0.0	11
		Unvegetated	30.9 \pm 0.3	12.4 \pm 1.3	0.0 \pm 0.0	11

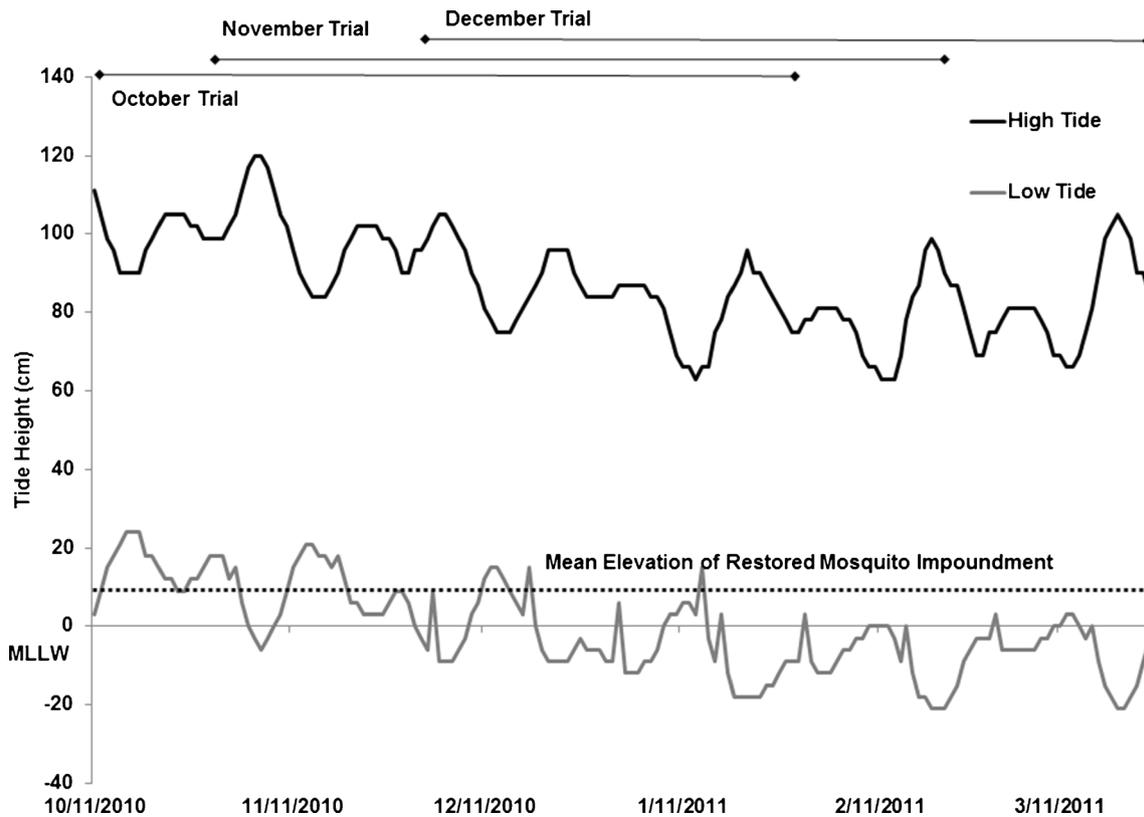


Fig. 2 The maximum tide height (cm; *solid black line*) and minimum tide height (cm; *solid gray line*) during the October, November, and December trials. The mean elevation of the mosquito impoundment

where the study was conducted is shown with the *black dotted line*. Tidal data was derived from predicted tidal heights for the Ponce Inlet, New Smyrna station and was retrieved from <http://tidesandcurrents.noaa.gov>

Results

The minimal adequate survival model retained the main effects of shoreline type and trial start date and the interaction term (Table 2). The scale was 1.49, indicating that hazard (or risk of loss) increased with time in our study and there was a significant effect of factors on propagule retention time ($\chi^2=264.8$, $df=5$, $p<0.001$). Propagules were lost faster at unvegetated shorelines compared to vegetated shorelines

during all trials (estimated effect size=2.75; $p<0.001$; Table 2). At all vegetated shorelines, vegetation was emergent at low tide and taller than propagules when in a vertical position (range of propagule lengths=28–36 cm; Table 1). All vegetated locations had 100 % cover in all 60 quadrats, and there was no significant difference in percent cover of *B. maritima* and *S. perennis* at the three locations. Mean percent cover ranged between 47 and 51 % for *B. maritima* and 49 and 53 % for *S. perennis* per location. At the end of the October trial, 44 of the original 60 propagules (73.3 %) remained in the vegetated shoreline, compared to 1 propagule (1.7 %) on unvegetated shorelines (Fig. 3). In the November trial, 42 propagules (70.0 %) were retained on the vegetated shoreline compared to only 6 propagules (10 %) at the unvegetated shoreline (Fig. 3). At the end of the December trial, 32 propagules (53.3 %) were retained in the vegetated area, compared to 1 propagule (1.7 %) at unvegetated shorelines (Fig. 3).

There were no significant contrasts among trial start dates, but there was a significant interaction for October trial and unvegetated shorelines compared to reference values of vegetated shorelines and December trial (estimated effect size=4.13; $p=0.003$, Table 2). Propagules from the October trial at the unvegetated shoreline treatment were lost faster than propagules in the November and December trials: 56 out of 60

Table 2 Model summary of survival analysis comparing retention time of *Rhizophora mangle* propagules between shoreline types (vegetated, unvegetated) and trial start dates (October, November, December). Reference values were December trial and vegetated shoreline treatment

	Value	SE	z	p
Intercept	5.63	0.29	19.31	<0.001
Trial: October	0.13	0.42	0.31	0.76
Trial: November	-0.02	0.41	-0.05	0.96
Shoreline type: unvegetated	-2.89	0.36	-8.07	<0.001
October: unvegetated	-1.50	0.50	-2.99	0.003
November: unvegetated	0.09	0.50	0.18	0.86
Log(scale)	0.40	0.05	8.52	<0.001

Model: Trial start date + Shoreline type + Trial start date × Shoreline type

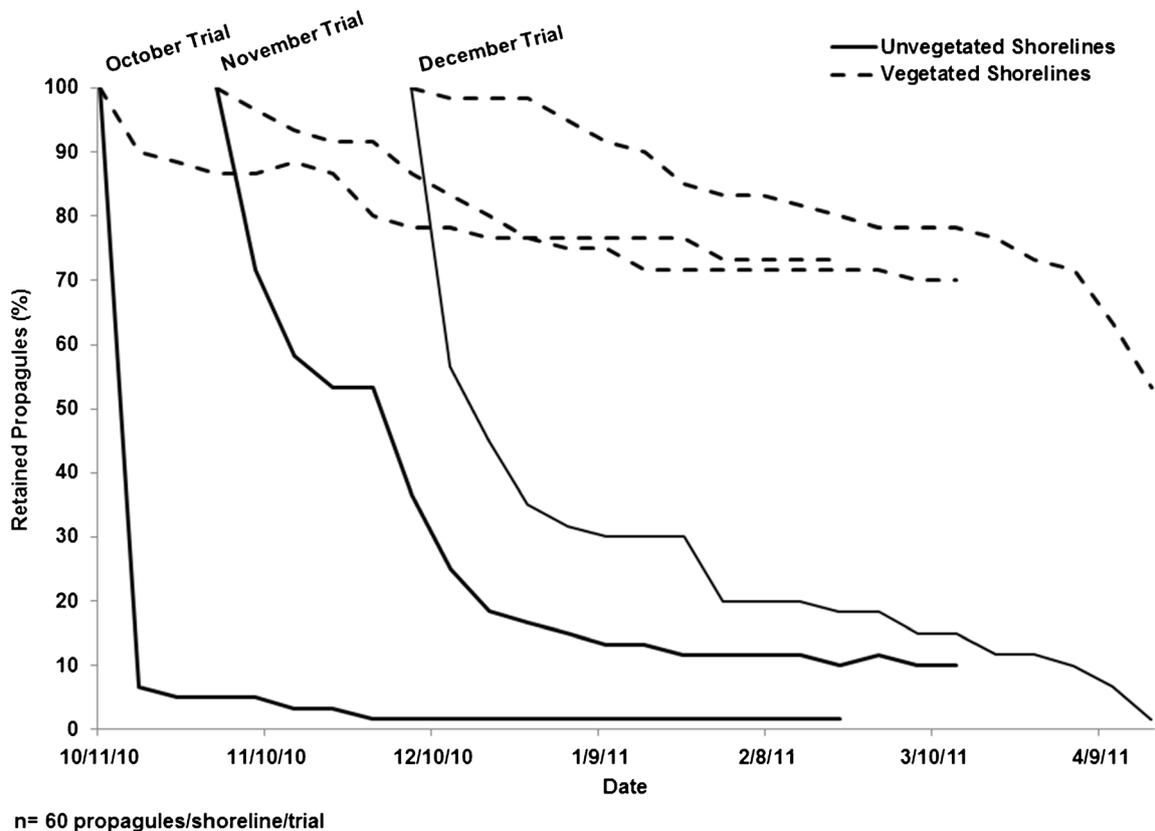


Fig. 3 Percent of *Rhizophora mangle* propagules retained at unvegetated shorelines (solid line) and vegetated shorelines (dashed lines) for trials initiated on 11 October 2010 (trial 1), 1 November 2010 (trial 2), and 3 December 2010 (trial 3). For each trial date, 60 propagules were dropped

on day 1 at each shoreline type (vegetated, unvegetated). There was a significant effect of factors on the retention of propagules (survival analysis: $\chi^2=264.8$, $df=5$, $p<0.001$)

propagules (93.3 %) were lost after 2 days (Fig. 3). Elevation in study plots was similar for all locations (~12 cm above MLLW; Table 1), and the length of propagules was similar between trial dates (Table 1). The October trial began during the beginning of high water season (initial mean water depth \pm SE = 4.7 ± 0.2 cm (vegetated shoreline) and 5.9 ± 0.3 cm (unvegetated shoreline) when propagules deployed; Table 1), and study plots were flooded during both high and low tides for an estimated 33 days throughout the 16-week experiment (Table 1). During the November trial setup, mean water depth \pm SE was 4.8 ± 0.3 cm at vegetated shoreline and 5.2 ± 0.3 cm at unvegetated shoreline, and study plots were inundated at high and low tides for an estimated 20 total days (Table 1). The December trial began near the end of high water season, and vegetated and unvegetated shoreline locations were not flooded during trial setup (Table 1). The estimated number of days of inundation at high and low tide was 11 days over the 16-week trial (Table 1).

At the start of October and November trials, propagules were dropped in a horizontal orientation at water surface; however, propagules shifted to an upright position with the posterior end of the propagule in contact with the substrate when unvegetated locations were flooded at initial setup. The

majority of propagules dropped at vegetated shorelines also shifted into the vertical position in the October and November trials (57 and 53 of the 60 propagules for each trial, respectively). During the setup of the December trial, propagules remained horizontal when dropped on the unvegetated substrate. In comparison, 41 of the 60 propagules dropped in the vegetation were in a vertical position once in contact with the vegetation. By the end of the three trials, all retained propagules in the vegetated shoreline treatments were in a vertical position and produced two leaves, whereas all propagules remaining in the unvegetated shorelines were in a horizontal position, showed signs of desiccation on the hypocotyl (brown and shriveled), and lacked development of leaves or roots.

Consumer damage to propagules during October and November trials was only observed in the vegetated treatment (32 (53.3 %) and 15 (25 %) propagules, respectively). Consumer damage was not always fatal in the vegetated shorelines, and 14 damaged propagules in the October trial and 10 damaged propagules in the November trial were retained and produced leaves by the end of the trial. Consumer damage during the December trial was observed on 12 (20 %) propagules in the vegetated shoreline and on the one remaining propagule in the unvegetated shoreline. Damage to the propagules on the

vegetated shoreline during final weeks of the December trial (when locations were experiencing less frequent periods of complete inundation) resulted in propagules broken into multiple sections.

Discussion

Facilitation by nurse plants through propagule trapping and support can have a positive effect on mangroves by increasing retention until rooting occurs at shorelines with frequent flooding, particularly in locations where the habitat is recovering from natural or anthropogenic disturbances (Lewis 1982; McKee et al. 2007). Our study found that the presence of *B. maritima* and *S. perennis* on shorelines had a significant positive effect on the retention time of *R. mangle* propagules, supporting a hypothesis that vegetation can increase retention time as a mechanism of facilitation by propagule trapping. In addition, only mangrove propagules in the vegetated treatments were in a vertical position, did not show signs of desiccation, and produced roots and initial leaves by the end of our study. We also observed natural recruitment of three native mangrove species (*R. mangle*, *A. germinans*, and *Laguncularia racemosa*) in the vegetated study plots during all three trials. Although propagules from the three species were also observed stranded in the unvegetated plots, we did not see any propagules develop into seedlings during our trials. Recruitment and growth of pioneer halophytes able to trap and support mangrove propagules may be a critical first step in secondary succession and recovery of mangrove communities at disturbed or restored coastal wetlands.

Mangrove dispersal in Mosquito Lagoon coincides with seasonal high water, and mechanisms increasing retention of propagules when shorelines are inundated can positively affect mangrove recruitment. There was a significant interaction between trial date and shoreline type, with the largest difference in time of retention observed in the October trial when propagules were subjected to an estimated 33 days of flooding at both high and low tides, compared to 20 and 11 days during the November and December trials, respectively (Fig. 2; Table 1). Although study plots were flooded during the setup of both the October and November trials (Fig. 2; Table 1), higher retention of propagules during the November trial may have been caused by the decrease in number of days study plots were inundated over the entire tidal cycle. The orientation of shorelines for the October and November trials was different from the December trial (Fig. 1), and differences in currents and wave energy may also account for some of the variation between trials. However, all sites were in a low-energy location, away from major boating channels, and the similarities in elevations of the sites (Table 1) suggest that wave energy and rates of erosion were similar among sites.

Mangrove propagules initiated root production and produced a first set of leaves when locations were experiencing frequently flooded conditions at vegetated shorelines. Our study suggests that propagules released from parental trees at the beginning of the high water season will particularly benefit from trapping in vegetation due to the extended inundation period; however, this mechanism may be less critical during the dry season in this microtidal estuary. In mesotidal estuaries with daily tidal fluctuations, the effect of propagule trapping may be greater due to more frequent inundation periods and increased chance of removal by tides after stranding; thus, comparative studies between mesotidal and microtidal wetlands would be useful in order to understand the effect of propagule trapping under different hydrodynamic conditions. The importance of facilitative interactions may increase as coastal wetlands experience effects of sea level rise, assuming that nurse plants will be able to tolerate rises in sea level (Gilman et al. 2008; Alongi 2009; McKee et al. 2012). Plant-plant interactions have a significant effect on plant community dynamics and may mediate some environmental changes caused by climate change or other anthropogenic threats (Brooker 2006; Padilla and Pugnaire 2006; Brooker et al. 2008). Climate changes can also interrupt some community interactions or intensify others, such as competition (Brooker 2006), and research evaluating synergistic effects of climate change and community interactions is needed to understand the role interactions have in the resistance and resilience of mangrove systems.

Propagule trapping specifically assists with retention of propagules during the post-dispersal stranding phase of a mangrove's life cycle; however, vegetation may have both direct and indirect effects on mangroves and may change with developmental stage. For example, vegetation may provide an indirect benefit to stranded propagules by shading them from direct sunlight and reducing mortality from desiccation (McKee et al. 2007). We found that propagules retained on the unvegetated shorelines suffered from desiccation, leading to the loss of viability by the end of trials when water levels decreased and sites were exposed to longer dry periods. In comparison, propagules on the vegetated shorelines did not show signs of desiccation, despite dry conditions at the end of the trials. McKee et al. (2007) also observed signs of desiccation in *R. mangle* propagules planted in bare patches in a recovering wetland in Belize. In addition to the benefits of shading to the propagules, vegetation also shades the soil and decreases rates of evaporation during dry periods (Bruno et al. 2003; Young et al. 2005), further reducing potential of desiccation to propagules and creating more favorable abiotic conditions once the propagules become rooted.

Growth and survival of mangrove seedlings once established on the shoreline will be affected by tolerances to local abiotic conditions and amelioration of limiting soil conditions by initial colonizers, which may indirectly facilitate

survival of seedlings (McKee et al. 2007). We compared vegetated shorelines to unvegetated shorelines in order to test a hypothesis of propagule trapping; however, the differences in plant distribution could have been caused by local conditions within the patches on the shorelines. At our study site, initial recruitment of *B. maritima* and *S. perennis* occurred through seed and fragment dispersal and extension of vegetative runners from the interior portion of the restored mosquito impoundment. Plant cover increased over time through vegetative propagation, resulting in vegetated patches surrounded by bare patches. Both species are halophytes with a high tolerance for salinity (Davy et al. 2006; Debez et al. 2010), and these two early successional species have been observed colonizing bare patches where salinity can increase to over 70 ppt during the dry season (soil salinities average 28 ppt year-round; unpublished data, Donnelly et al.). After colonization, vegetated areas at restored mosquito impoundments have significantly lower soil salinities (10–20 ppt less) compared to unvegetated areas (unpublished data, Donnelly et al.). This was similar to findings by McKee et al. (2007) in Belize where decreased soil salinity and temperature were observed in vegetated patches compared to bare patches. Once established, long-term survival of mangroves seedlings will also be affected by other biotic interactions, including competition for light and nutrients with neighboring plants (McKee 1995; Bruno et al. 2003; Young et al. 2005; Stevens et al. 2006; McKee et al. 2007). Our study focused on the effect of vegetation on initial establishment of mangroves at restored locations and ended after 16 weeks; therefore, long-term effects of early colonizing species on mangrove survival after the establishment phase are beyond the scope of our study, and additional studies are needed to further investigate the role of facilitative interactions in coastal wetland succession.

Negative biotic interactions, such as damage by crabs, insects, and other consumers, also strongly influence mangrove seedling establishment and distribution within a coastal wetland (Robertson et al. 1990; Rey 1994; McKee 1995; Minchinton and Dalby-Ball 2001; Stevens et al. 2006). Although not a primary objective for this study, we observed herbivore damage to mangrove propagules in the vegetated shorelines, including bite marks, entrance, and exit holes of suspected Lepidopteran larvae, and propagules broken into multiple pieces. Propagule damage was only observed on the one remaining propagule in the unvegetated treatment during the December trial, but this difference can be a result of the short time period most propagules were retained rather than a difference in shoreline type. However, nurse plants may serve as refugia for consumers (Padilla and Pugnaire 2006), and propagule damage was a cause of mortality at the vegetated shorelines. Consumer damage did not prevent establishment of seedlings at vegetated shorelines, and the overall effect of vegetation on propagule retention and establishment was positive in all trials. In comparison, the small number of

propagules retained in the unvegetated treatments did not transition to the seedling stage despite lack of damage by consumers.

Our results support a hypothesis of propagule trapping as an important facilitative mechanism for recruitment of *R. mangle* to subtropical coastal wetlands following water dispersal and also identify additional questions for future research. First, longer studies are needed to investigate the effect of early successional species on *R. mangle* after seedling establishment and the long-term effect on coastal wetland succession. Second, the size of propagules may influence the success of propagule trapping; however, we did not tag propagules prior to deployment in the field, and we could not include the propagule length in our statistical analysis as a potential factor on retention time. Third, our method of dropping propagules into the middle of the study plots was chosen because it mimics methods used by restoration practitioners. Thick patches of vegetation may impede mangrove propagules from moving into vegetation with tides (Peterson and Bell 2012); however, we observed natural dispersal of mangrove propagules into the interior portion of the vegetation patches during this study, possibly as a result of stranding during high tides when vegetated shorelines were completely submerged. Studies using a more natural method of introducing propagules would be helpful to further investigate the effects of propagule trapping on naturally dispersing propagules. Fourth, species present in different locations may have different effects on mangrove propagule trapping. In contrast to the trapping of *R. mangle* propagules by *B. maritima* documented in this study, Peterson and Bell (2012) found that *B. maritima* did not have a positive effect on retention of smaller *A. germinans* propagules. McKee et al. (2007) also found differences in the effects of nurse plant species in Belize, and these results suggest that species-specific characteristics may be important in evaluating the importance of propagule trapping on mangrove species. Finally, the positive effect of vegetation on mangroves, particularly those occurring during the initial colonization and establishment stages, has direct applications to coastal wetland restoration, and studies combining facilitative interactions and coastal wetland restoration applications are needed.

Our study documented that over 50 % of propagules dropped into the vegetated area were retained and survived to the seedling stage, which is a higher survival rate of propagules than many other mangrove restoration projects where survival and retention of propagules and small seedlings often range between 1 and 20 % (Gilman and Ellison 2007; Salgado Kent and Lin 1999; Lewis 2005; Samson and Rollon 2008; Kamali and Hashim 2011). Applying facilitation concepts to restoration has the potential to increase project success, particularly in systems where physiological stress is high (Bruno et al. 2003; Padilla and Pugnaire 2006; Halpern et al. 2007; Peterson and Bell 2012). In riparian and wetland habitats,

restoration methods utilizing natural dispersal through hydrochory can be applied to larger areas, completed with lower project and labor costs, and maintain local genetic variation and adaptations (Nilsson et al. 2010). Hydrological restoration of coastal wetlands by removing barriers to tidal influence has been shown to promote growth of halophytic species and natural dispersal of mangrove propagules, developing a diverse plant community without the need for additional planting (Brockmeyer et al. 1997; Turner and Lewis 1997; Lewis 2005; Nilsson et al. 2010; Rey et al. 2012). When natural regeneration is not possible due to recruitment limitations, planting propagules or seedlings in existing vegetation may increase establishment compared to planting in unvegetated locations (Young et al. 2005; Milbrandt and Tinsley 2006; Peterson and Bell 2012). An ecosystem-level approach that addresses both biotic and abiotic interactions affecting mangrove recruitment, survival, and growth is necessary to increase success of mangrove restoration projects and conserve remaining mangrove ecosystems.

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